

KLEPTOPARASITISM AND CANNIBALISM IN A COLONY OF LESSER KESTRELS (*Falco naumanni*)

JUAN JOSÉ NEGRO, JOSÉ ANTONIO DONÁZAR AND FERNANDO HIRALDO
Estación Biológica de Doñana, CSIC, Apdo, 1056, 41080 Seville, Spain

ABSTRACT.—We describe kleptoparasitism and cannibalism for the first time in a colony of Lesser Kestrels (*Falco naumanni*). Kleptoparasitism was practiced almost exclusively by females, the larger sex, while males received most of the attacks. Kleptoparasitic Lesser Kestrels had a relatively high success (43.1%, $N = 52$ attempts) compared to other species in which kleptoparasitism occurs frequently. Two cases of chick cannibalism by adults were also recorded.

Cleptoparasitismo y canibalismo en una colonia de Cernícalos Primillas (*Falco naumanni*).

EXTRACTO.—El cleptoparasitismo y el canibalismo han sido observados por vez primera en una colonia de Cernícalos Primillas (*Falco naumanni*). El cleptoparasitismo fue practicado casi exclusivamente por hembras, que son de mayor tamaño que los machos, mientras que éstos recibieron la mayoría de los ataques. El éxito de los ataques fue relativamente alto (43.1%, $N = 52$ intentos) en comparación con el observado en otras especies donde el cleptoparasitismo es frecuente. También registramos dos casos de canibalismo practicado contra pollos por Cernícalos Primillas adultos.

Despite the fact that kleptoparasitism has been reported in several birds of prey (for a review see Brockman and Barnard 1979), it seems to be rare among species of the genus *Falco*. The Lesser Kestrel (*Falco naumanni*) is a colonial small falcon. Although both sexes do not show significant differences for most body traits, females are up to 24% heavier than their mates (Cade 1982). Males feed their females from before to a few days after egg laying, share incubation and deliver most of the nourishment for their offspring (Donazar et al. 1992). None of the authors who have studied the species described kleptoparasitic behavior (see Glutz et al. 1971, Cramp and Simmons 1980). In this study we describe the occurrence of kleptoparasitism in a colony of Lesser Kestrels and discuss the role of the reversed size dimorphism (RSD) exhibited by the species in the directionality of the kleptoparasitic attacks. Additionally, we comment on two cases of chick cannibalism by adult Lesser Kestrels.

STUDY AREA AND METHODS

The observations were carried out during 1989 and 1990 in a colony of Lesser Kestrels nesting in Mairena del Alcor (37°22'N 5°45'W), Seville, southern Spain. We counted 42 breeding pairs in 1989 and 40 in 1990. A sample of nests in two adjacent walls of a tower was selected for systematic recording of behavior (see Negro et al. 1992 for details). The portion of the colony observed consisted of 7 nests in 1989 and 6 nests in 1990 (26 focal

individuals). The observations of behavioral interactions, feedings and the type of prey delivered were carried out from a distance of 70 m with a telescope (20–40×). The observations lasted from dawn to dusk, 2–3 d a week, from the beginning of the period of pair formation (February) until the independence of the fledglings (end of July). Observations amounted to 475 hr in 1989 and 567 hr in 1990. Simultaneously, one or two additional observers radiotracked seven males and six females which were breeding in the portion of the colony under observation. Radiotracking amounted to 305 hr in 1989 and 647 hr in 1990.

All the nests in the colony were visited 1–3 times during the breeding season. Adults were trapped on the nest and were banded with laminated plastic bands (wearing two characters) which allowed them to be identified by telescope. In 1989 a quarter of the adult Lesser Kestrels wore these bands and in 1990 the proportion was two-thirds of the adults in the colony. All the young in the colony were also marked with plastic bands in the two years of the study.

RESULTS

Food Supply. The availability of food in the environment was determined indirectly using feeding of nestlings as an approximate measure. The frequency of chick feedings in the colony was 1.8 feedings/hr in 1989 and 1.9 feedings/hr in 1990. Both values are below those observed in southern France (2 feedings/hr during 5.5 hr of observation; Blondel 1964 or 3.1 feedings/hr during 22.7 hr; Hovette 1971) and in northeastern Spain (5.4 feedings/hr

during 6.7 hr; M. Pomarol pers. comm.). Our values are higher, however, than those given by Bijlsma et al. (1988) for colonies in Extremadura in southwestern Spain (1.3 feedings/hr during 26 hr) where, according to the authors, the availability of food was very high. Nonetheless, these authors collected their data at the beginning of the post-fledging period, when the rate of feeding of the young is reduced (Bustamante 1990).

The prey consumed in our area might have been smaller than prey in the other studies. Most prey were insects. The percentage of vertebrates was low (0.9% of 1113 items) compared to 6.3% vertebrates observed by Franco and Andrada (1977) in the same general area several years ago, 2.6% observed in Provence (Hovette 1971), and 5.7% observed in Extremadura (Bijlsma et al. 1988).

Kleptoparasitism and Cannibalism. At least 4 individuals from the colony, but only 1 of the 26 focal individuals acted as kleptoparasites. Kleptoparasitic attacks were directed at 14 (53.8%) of these 26 focal birds. Kleptoparasitism occurred during the chick rearing period (June–July), when the parents delivered prey directly to their young in the nest. As they perched in the entrance of the nest, the attacker flew in and tried to snatch the food. Kleptoparasitic attacks were never observed while radiotracking the birds in the hunting areas, nor during the period of mate-feeding (April–May; see Donázar et al. 1992). Of the 51 attempts at stealing food, 29 (57%) failed. Of these failed attempts, 14 (48%) were because of the aggressive response by the victim, 13 (44%) were because the adult managed to transfer the food to the chicks and two (6.9%) were because the victim appeared to have anticipated the attack and escaped without feeding the chicks (although they returned later on).

Males fed chicks more than females in the period during which kleptoparasitism occurred (61.5% vs. 38.5%, $N = 894$ feedings); they were also the victims of a disproportionate number of the kleptoparasitic attacks (82.4% vs. 17.6%, $N = 51$; $\chi^2 = 9.004$, $P = 0.002$). Females were responsible for the majority of attacks (94%). Of the others, two attacks (3.9%) were made by males and one by a bird of unknown sex (goodness of fit test assuming sex ratio of 1:1, $\chi^2 = 40.50$, $P < 0.001$). When the attacker was a female, success tended to be higher when attacking males (45.2%, $N = 41$) than when attacking females (14.2%, $N = 7$), although the difference was not significant (Fisher's exact test, $P > 0.05$).

One banded female (CK) carried out 62% of the attacks. She attacked at least nine different males and four females. Another two identified females carried out one and two of the attacks, respectively. Banded but not identified females (possibly CK) carried out 13 attacks (25.4%). Another two attacks were carried out by a male and a third by an individual of unknown sex.

The importance of kleptoparasitism for the feeding of the female CK may be greater than that observed. Her nest, although near, was in a different portion of the colony so she may have made attacks which we did not observe. This female was the most successful breeder in the colony in the two years of the study. In 1989, she successfully reared three chicks when the average number of chicks fledged per breeding pair in the colony was 1.8 ± 0.17 ($N = 42$ pairs). In 1990, she successfully reared four chicks, when the average per pair in the colony was 1.4 ± 0.88 ($N = 39$ pairs).

The parasitic activity of CK was not limited to stealing food from adults carrying prey to the nest. On one occasion the fresh carcass of a 7-day-old chick, which did not correspond to any of her young, was found in her nest. On another occasion, CK was seen trying to steal a chick 10 d old from a nest. This attempt was prevented by the parent female when CK had already managed to take the chick out of the nest entrance. CK's objective was evidently the chick as she fought violently with the resident female for its possession. In 1991, we observed one adult male stealing and eating a chick in a neighboring colony.

DISCUSSION

Our data suggest that the food supply to the young by parent Lesser Kestrels was lower in the studied colony than that encountered by other investigators several decades ago in the same area or in other regions in the Western Palearctic. Additionally, we observed a high nestling mortality (about 50%) in the two years of study due to starvation (Negro 1991). Such high mortality rates have not been observed by other investigators cited here and they seem to be uncommon among raptors of similar size (e.g., Newton 1979). Both lines of evidence, the low provisioning rate and the high nestling mortality, suggest that the period of study was a time of food shortage for the Lesser Kestrels. Kleptoparasitism and cannibalism have been said to be favored in stressful

food conditions (Brockmann and Barnard 1979, Jorde and Lingle 1988, Jones and Mañez 1990, Bortolotti et al. 1991).

Kleptoparasitism was practiced mainly by female Lesser Kestrels, the larger sex, with most attacks made on males. In other species, size is apparently a determining factor for success in kleptoparasitic attempts (Knight and Knight 1988, Tershy and Breese 1990). If the frequency of kleptoparasitic attempts is influenced by the RSD (i.e., the larger size of the females) in the Lesser Kestrel, it would also be expected that males were the subject of successful attacks more frequently than females. Our results do not show a clear tendency in this respect, although this could be due to the low frequency of attacks by females on other females. It might also be that, since females spent more time in the colony throughout the breeding cycle (Donázar et al. 1992), they would have more opportunities to carry out kleptoparasitic attempts. However, the attacks were, in the main, produced at the end of the nestling period when males and females spent a similar amount of time in the colony, and not in other periods of the breeding cycle when the females' colony attendance was higher than that of males. Kleptoparasitism was practiced by a few individuals, such as the female CK, who apparently had specialized in this behavior. The systematic kleptoparasitism by the female CK may have been highly profitable, given her high reproductive success in both years of the study. We cannot discount, however, that other factors were involved, such as a high provisioning rate of her mate.

Lesser Kestrels had a relatively high success rate in their kleptoparasitic attempts (43.1%). Other species practicing intraspecific kleptoparasitism showed lower figures: Common Tern (*Sterna hirundo*) 6.2% (Hopkins and Willey 1972), Bald Eagle (*Haliaeetus leucocephalus*) 8.1% (Fischer 1985), Black Kite (*Milvus migrans*) 3.4–16.6% (Sunyer 1988). In other raptor species where intraspecific kleptoparasitism is widespread, individuals use display behaviors to hide the prey and deceive potential pirates (Brown 1976, Fischer 1985, Sunyer 1988). Such patterns of behavior were not evident in the case of the Lesser Kestrels (only 4% of the victims apparently detected the attacker). Nevertheless, in 1990 we twice observed atypical behavior by two individuals that had been recently kleptoparasitized. These males circled over the colony before feeding the chicks, and then dived to the nest.

ACKNOWLEDGMENTS

M. de la Riva assisted in the field work. S. Flemming and W.M. Iko helped us revise the manuscript. A. Krupa helped to translate an early Spanish draft. The CSIC-CICYT provided financial support (project PB87-0405).

LITERATURE CITED

- BIJLSMA, S., E.J.M. HAGEMEIJER, G.J.M. VERKLEY AND R. ZOLLINGER. 1988. Ecological aspects of the Lesser Kestrel *Falco naumanni* in Extremadura (Spain). Rapport 285, Katholieke Universiteit Nijmegen, The Netherlands.
- BLONDEL, J. 1964. Notes sur la biologie et le régime alimentaire du Faucon Crécerellette *Falco naumanni*. *Nos Oiseaux* 28:295–296.
- BORTOLOTTI, G.R., K.L. WIEBE AND W.M. IKO. 1991. Cannibalism of nestling American Kestrels by their parents and siblings. *Can. J. Zool.* 69:1447–1453.
- BROCKMANN, H.J. AND C.J. BARNARD. 1979. Kleptoparasitism in birds. *Anim. Behav.* 27:487–514.
- BROWN, L.H. 1976. Birds of prey, their biology and ecology. Hamlyn Publication Co., London, U.K.
- BUSTAMANTE, J. 1990. Condicionantes ecológicos del período de emancipación en Falconiformes. Disertación doctoral. Universidad Autónoma de Madrid, Madrid, Spain.
- CADE, T.J. 1982. The falcons of the World. Cornell University Press, Ithaca, NY.
- CRAMP, S. AND K.E.L. SIMMONS. 1980. The birds of the Western Palearctic. Vol. 2. Oxford University Press, Oxford, U.K.
- DONÁZAR, J.A., J.J. NEGRO AND F. HIRALDO. 1992. Functional analysis of mate-feeding in the Lesser Kestrel *Falco naumanni*. *Ornis Scandinavica* 23:190–194.
- FISCHER, D.L. 1985. Piracy behavior of wintering bald eagles. *Condor* 87:246–251.
- FRANCO, A. AND J. ANDRADA. 1977. Alimentación y selección de presa en el *Falco naumanni*. *Ardeola* 23:137–187.
- GLUTZ, U.N., K.M. BAUER AND E. BEZZEL. 1971. Handbuch der Vögel Mitteleuropas. Vol. 4. Akademische Verlagsgesellschaft, Frankfurt, Germany.
- HOPKINS, C.D. AND R.H. WILEY. 1972. Food parasitism and competition in two terns. *Auk* 89:583–594.
- HOVETTE, C. 1971. Notes sur la reproduction du Faucon Crécerellette *Falco naumanni* en Provence. *Nos Oiseaux* 31:82–90.
- JONES, A.M. AND M. MAÑEZ. 1990. Cannibalism by Black Kite (*Milvus migrans*). *J. Raptor Res.* 24:28–29.
- JORDE, D.G. AND G.R. LINGLE. 1988. Kleptoparasitism by Bald Eagles wintering in south-central Nebraska. *J. Field Ornithol.* 59:183–188.
- KNIGHT, R.L. AND S. KNIGHT. 1988. Agonistic asymmetries and the foraging ecology of Bald Eagles. *Ecology* 69:1188–1194.
- NEGRO, J.J. 1991. Ecología de poblaciones del cernícalo

- primilla *Falco naumanni*. Disertación doctoral. Universidad de Sevilla, Sevilla, Spain.
- , J.A. DONÁZAR AND F. HIRALDO. 1992. Copulatory behavior in a colony of Lesser Kestrels: sperm competition and mixed reproductive strategies. *Anim. Behav.* 43:921–930.
- NEWTON, I. 1979. Population ecology of raptors. T. and A.D. Poyser, Ltd., Berkhamsted, U.K.
- SUNYER, C. 1988. El cleptoparasitismo en el Milano Negro. M.Sc. thesis. Universidad Complutense de Madrid, Madrid, Spain.
- TERSHEY, B.R. AND D. BREESE. 1990. The influence of sexual dimorphism on kleptoparasitism of Blue-footed Boobies by Brown Boobies. *Can. J. Zool.* 68:197–199.

Received 6 February 1992; accepted 1 May 1992